

Predator confusion is sufficient to evolve swarming

Randal S. Olson ^{* †}, Arend Hintze ^{‡ †}, Fred C. Dyer ^{§ †}, David B. Knoester ^{‡ †}, and Christoph Adami ^{‡ †}

^{*}Department of Computer Science and Engineering, Michigan State University, East Lansing, MI 48824, USA, [†]Department of Microbiology and Molecular Genetics, Michigan State University, East Lansing, MI 48824, USA, [‡]Department of Zoology, Michigan State University, East Lansing, MI 48824, USA, and [§]BEACON Center for the Study of Evolution in Action, Michigan State University, East Lansing, MI 48824, USA

Submitted to Proceedings of the National Academy of Sciences of the United States of America

Swarming behaviors in animals have been extensively studied due to their implications for the evolution of cooperation, social cognition, and predator-prey dynamics. An important aspect of these studies is discerning which evolutionary pressures favor the formation of swarms. One hypothesis is that swarms arise because the presence of multiple moving prey in swarms causes confusion, but it remains unclear how important this selective force is. Using a model of a predator-prey system with evolving predator and prey behaviors, we show that predator confusion provides a sufficient selection pressure to evolve swarming behavior in prey. Furthermore, we demonstrate that the evolutionary effect of predator confusion on prey could in turn exert evolutionary pressure on the structure of the predator's visual field, favoring the frontally oriented, high resolution visual systems commonly observed in predators that feed on swarming animals. Finally, we provide evidence that when prey evolve swarming in response to predator confusion, there is a change in the shape of the functional response curve describing the predator's consumption rate as prey density increases. Thus, we show that a relatively simple perceptual constraint—predator confusion—could have pervasive evolutionary effects on prey behavior, predator sensory mechanisms, and the ecological interactions between predators and prey.

swarm behavior | confusion effect | evolution | functional response

The sudden emergence of a cohesive swarm from the erratic movements of individual animals is one of nature's most striking examples of collective animal behavior [1]. For example, European starlings (*Sturnus vulgaris*) are known to form spectacular, coordinated flocks composed of hundreds of thousands of birds, seemingly without any form of leadership [2]. During their monthly breeding seasons, Atlantic herring (*Clupea harengus*) aggregate into schools comprising hundreds of millions fish to defend themselves against predators [3]. Perhaps most notoriously, desert locusts (*Schistocerca gregaria*) form massive swarms with billions of locusts that devastate entire agricultural zones in Africa, the Near East, and southwest Asia [4].

While swarm-like aggregations could arise for relatively simple reasons, e.g., to converge on a common resource [5], in many cases swarms are formed via behavioral mechanisms that coordinate the movements of individuals to ensure group cohesion [6]. Since swarming may incur a variety of fitness costs, considerable effort has been devoted to understanding the compensatory benefits of swarming [7]. Many such benefits have been proposed: swarming may improve mating success [8,9], increase foraging efficiency [10], and provide distributed information processing abilities [1]. In this study, we focus on swarming as a defense against predation [7].

Evolved swarm behaviors protect group members from predators in several ways. For example, swarming improves group vigilance [11–14], reduces the chance of being encountered by predators [14,15], dilutes an individual's risk of being eaten [16–18], enables an active defense against predators [19], and reduces predator attack efficiency by confusing the predator [20,21]. Given the long generation times of the animals involved (months to years), it is exceedingly difficult to discern which of these benefits, if any, are sufficient to produce swarming as an evolutionary response, let alone study the properties of swarm behaviors once they have arisen [21,22].

To address this challenge, we experimentally investigate the evolutionary origins of swarming behavior in a digital system. Digital systems have previously been used to provide key insights into core evolutionary processes [23,24], and several well-known studies have adopted digital systems as a method to study swarm behavior [6,25–27]. These previous studies have provided exciting insights into the fundamental dynamics of swarming behavior, but have not focused on isolating the evolutionary pressures that might favor the formation of swarms. In fact, these studies typically have not studied Darwinian evolution as a process affecting the properties of swarms. Here, we present a model in which predators and groups of genetically homogeneous prey are coevolved in a two-dimensional virtual environment. Predators are endowed with a retina that enables them to observe prey, while prey are equipped with a retina that enables them to sense both conspecifics and predators. In this model, predator and prey are preferentially selected based on how effective they are at consuming prey and surviving, respectively. Swarming is a possible solution for the prey, but is not selected for directly.

Within this digital environment, we specifically study the evolution of swarming in the presence of *predator confusion*, where the presence of multiple individuals moving in a swarm is believed to confuse approaching predators, making it difficult for them to successfully execute an attack [20,21,28,29]. In a recent review of predator-prey systems with swarming prey, Jeschke noted that predators appeared to become confused by swarming behavior in 16 of the 25 systems reviewed [21], thus the seemingly-widespread mechanism of predator confusion merits further investigation as a selective force favoring the evolution of swarming behavior.

Predator confusion is broadly interesting for two additional reasons. First, it provides an opportunity to study how swarming behavior can exert evolutionary pressures on predators, especially on the perceptual constraints that allow for predator confusion in the first place. It is plausible that once swarming behavior evolves in prey, predator confusion may in turn provide a selective advantage for predators that are no longer confused by swarms. Second, predator confusion may influence the *functional response* describing the predator's consumption rate as prey density increases [30], as suggested in a previous study [21]. Understanding how pervasive mechanisms such as predator confusion affect functional response relationships is critical for accurately modeling

Reserved for Publication Footnotes

the dynamics of predator-prey interactions over ecological and evolutionary time [31].

Methods

To study the effects of predator confusion on the evolution of swarming, we developed an agent-based simulation in which predator and prey agents interact in a continuous two-dimensional virtual environment. All agents are controlled by stochastic state machines called Markov Network Brains (MNBs) [32], which make control decisions based on a combination of sensory input (i.e., vision) and internal states (i.e., memory). We coevolve the MNBs of predators and prey with a genetic algorithm, selecting for MNBs that exhibit behaviors that are more effective at consuming prey and surviving, respectively. Certain properties of the sensory and motor behavior of predators and prey are implemented as constraints that model some of the differences between predators and prey observed in nature (e.g., relative movement speed, turning agility, and, for predators, maximum consumption rate). Predator confusion, described in more detail below, is implemented as a constraint on predator perception that can be varied experimentally. In the remainder of this section, we summarize the evolutionary process that enables the coevolution of predator and prey, describe the sensory-motor architecture of individual agents, then present the characteristics of the environment in which predator and prey interact. A detailed description of MNBs and how they are evolved can be found in the SI text.

Coevolution of predator and prey. We coevolve the predator and prey with a *genetic algorithm* (GA), which is a digital model of evolution by natural selection [33]. In a GA, pools of genomes are evolved over time, by evaluating the fitness (the phenotype) of each genome at each generation and preferentially selecting those with higher fitness to populate the next generation. The genomes here are variable-length strings of integers that are translated into MNBs during fitness evaluation (see SI text). To perform this coevolution, we create separate genome pools for predator and prey genomes, and evaluate their fitness by selecting pairs of predator and prey genomes at random without replacement and place each pair into a simulation environment to be evaluated for 2,000 simulation time steps. Within this simulation environment, 50 identical prey agents are generated from the single prey genome, and competed with the single predator agent to obtain their respective fitness. This evaluation period is akin to the agents' lifespan, hence each agent has a potential lifespan of 2,000 time steps. The fitness values (calculated using the fitness function described below) are used to determine the next generation of the respective genome pools. Parameters describing the operation of this GA are summarized in Table S3. At the end of the lifetime simulation, we assign the predator and prey genomes separate fitness values according to the fitness functions:

$$W_{\text{predator}} = \sum_{u=1}^{2,000} S - A_u \quad [1]$$

$$W_{\text{prey}} = \sum_{u=1}^{2,000} A_u \quad [2]$$

where u is the current simulation time step, S is the starting swarm size (here, $S = 50$), and A_u is the number of prey agents alive at simulation time step u . Thus, predators are awarded higher fitness for killing more prey faster,

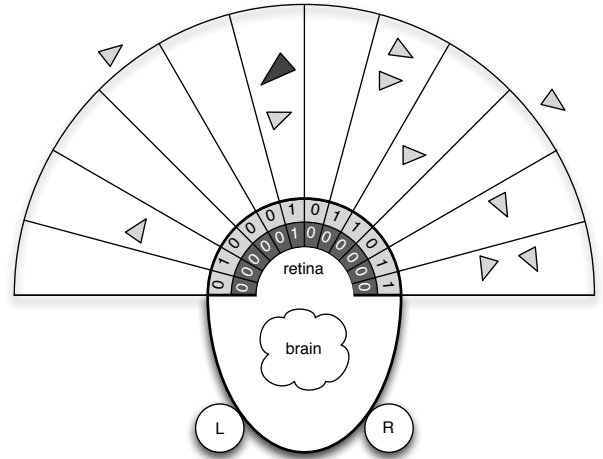


Fig. 1. An illustration of the predator and prey agents in the model. Light grey triangles are prey agents and the dark grey triangle is a predator agent. The predator and prey agents have a 180° limited-distance retina (100 units for the prey agents; 200 units for the predator agent) to observe their surroundings and detect the presence of the predator and prey agents. Each agent has its own Markov Network Brain, which decides where to move next based off of a combination of sensory input and memory. The left and right actuators (labeled "L" and "R") enable the agents to move forward, left, and right in discrete steps.

and prey are rewarded for surviving longer. Once we evaluate all of the predator-prey genome pairs in a generation, we perform fitness-proportionate selection on the populations via a Moran process, increment the generation counter, and repeat the evaluation process on the new populations until the final generation (1,200) is reached.

We performed 180 replicates of each experiment, where for each replicate we seed the prey population with a set of randomly-generated MNBs and the predator population with a pre-evolved predator MNB that exhibits rudimentary prey-tracking behavior. Seeding the predator population in this manner only serves to speed up the coevolutionary process, and has negligible effects on the outcome of the experiment (Figure S5).

Predator and prey agents. Figure 1 depicts the sensory-motor architecture of predator and prey agents in this system. Prey agents sense the predator and conspecifics with a limited-distance (100 units), pixelated retina covering its frontal 180° visual field. Its retina is split into 12 even slices, each covering an arc of 15°, representing the wide, coarse-grain visual systems typical in swarming birds [34]. Regardless of the number of agents present in a single retina slice, the prey agent only knows whether a predator, a conspecific, or both agent types reside within that slice, but not how many. For example in Figure 1, the furthest-right retina slice has two prey in it (light grey triangles), so the prey sensor for that slice activates. Similarly, the sixth retina slice from the left has both a predator (dark grey triangle) and a prey (light grey triangle) agent in it, so both sensors activate and inform the MNB that one or more predators *and* one or more prey are currently in that slice. Lastly, since the prey near the 4th retina slice from the left is just outside the range of the retina slice, the prey sensor for that slice does not activate. Once provided with its sensory information, the prey agent chooses one of four discrete actions: (1) stay still; (2) move forward 1 unit; (3) turn left 8° while moving forward 1 unit; or (4) turn right 8° while moving forward 1 unit.

Likewise, the predator agent detects nearby prey agents using a limited-distance (200 units), pixelated retina covering

its frontal 180° that functions just like the prey agent's retina. Similar to the prey agents, predator agents make decisions about where to move next, but the predator agent moves 3x faster than the prey agent and turns correspondingly slower (6° per simulation time step) due to its higher speed.

Simulation environment. We implemented a simulation environment to evaluate the relative performance of the predator and prey agents. At the beginning of every simulation, we place a single predator agent and 50 prey agents at random locations inside a closed 512 × 512 two-dimensional simulation environment. Each of the 50 prey agents are controlled by clone MNBs of the particular prey MNB being evaluated.

During each simulation time step, all agents are given their sensory input, update their MNB, then make a decision about where to move next. When the predator agent moves within 5 units of a prey agent it can see, it automatically makes a kill attempt on that prey agent. If the kill attempt is successful, the target prey agent is removed from the simulation and marked as dead. Predator agents are limited to one kill attempt every 10 simulation time steps, which is called the *kill delay*. The kill delay represents handling time after the successful prey capture, or the time it takes to refocus on another prey in the case of an unsuccessful attack. Shorter kill delays had negligible effects on the outcome of the experiment (Figure S6).

To investigate predator confusion as an indirect selection pressure driving the evolution of swarming, we implemented a perceptual constraint on the predator agent. When the predator confusion mechanism is active, the predator agent's chance of successfully killing its target prey agent (P_{kill}) is diminished when any prey agents near the target prey agent are visible anywhere in the predator's visual field. This is similar to previous models of predator confusion based on observations from natural predator-prey systems [21,35], where the predator's *attack efficiency* was reduced when attacking swarms of higher density. P_{kill} is determined by the equation:

$$P_{kill} = \frac{1}{A_{NV}} \quad [3]$$

where A_{NV} is the number of prey agents that are visible to the predator (i.e., in the predator agent's visual field) and are near the target prey (within 30 units; this includes the target prey itself). By only counting prey near the target prey, this mechanism localizes the predator confusion effect to the current target prey. Following this equation, the predator has a 50% chance of making a kill with one visible prey near the target prey, a 33% chance of making a kill with two visible prey near the target prey, etc. As a consequence, prey are in principle able to exploit predator confusion by swarming.

Results

Effects of Predator Confusion. Qualitatively, we observed significant differences in prey behavior over the course of evolution between swarms experiencing predators with and without predator confusion. Figure 2A illustrates that prey hunted by a predator without the predator confusion mechanism dispersed as much as possible to escape the predator. No replicates containing a predator without predator confusion resulted in prey behavior that resembled cohesive swarm behavior. In fact, each individual prey moved away from the predator, with no coherent swarm behavior visible. Conversely, when evolution occurred with predator confusion, prey exhibited cohesive swarm behavior in the majority of the replicates (70% of our replicates; Mann Whitney Rank Sum test between

predator confusion and non-predator confusion experiments at generation 1,200, $P = 2.42 \times 10^{-29}$). Figure 2B depicts one such swarm, where the prey agents formed multiple independent swarms to protect themselves against the predator agent's attacks.

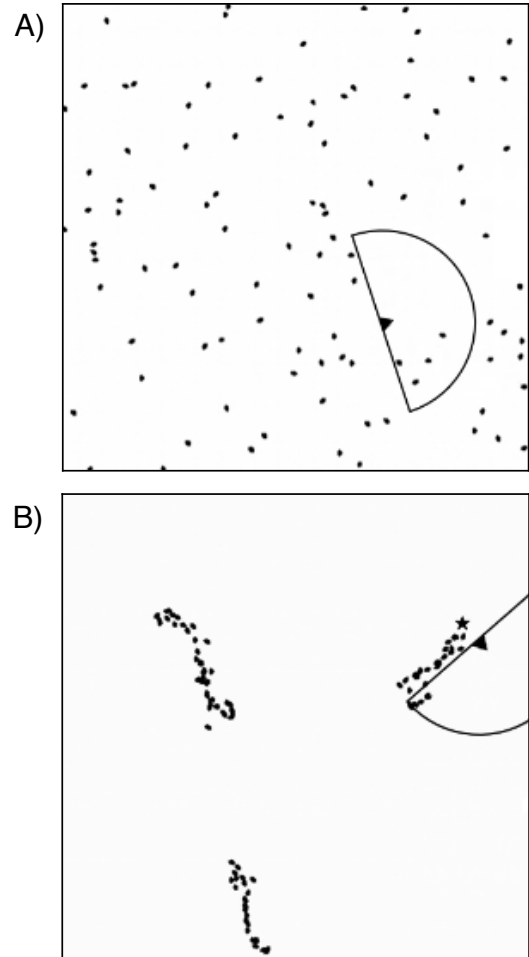


Fig. 2. Screen captures of (A) dispersed prey agents in a swarm hunted by a predator without the predator confusion mechanism and (B) prey agents forming multiple cohesive swarms to defend themselves from a predator with the predator confusion mechanism, after 1,200 generations of evolution. Black dots are prey agents, the triangle is the predator agent, the lines projecting from the predator agent represent the predator agent's frontal 180° visual field, and the star denotes where a prey agent was just killed.

Furthermore, the predator agents exhibited divergent hunting behaviors when hunting prey with and without the predator confusion mechanism active. As seen in Figure 2A, predators that evolved in the absence of predator confusion, and hence had to contend with dispersed prey, simply tracked the nearest visible prey until it was captured, then immediately pursued the next nearest visible prey. On the other hand, predators that evolved in the presence of predator confusion, and hence were challenged with cohesive swarms, used a strategy of attacking prey on the outer edges of the swarm. This strategy is similar to a predatory behavior observed in many natural systems [37,38], and effectively minimized the number of prey in the predator's retina and maximized its chance of making a kill. Figure 2B demonstrates this behav-

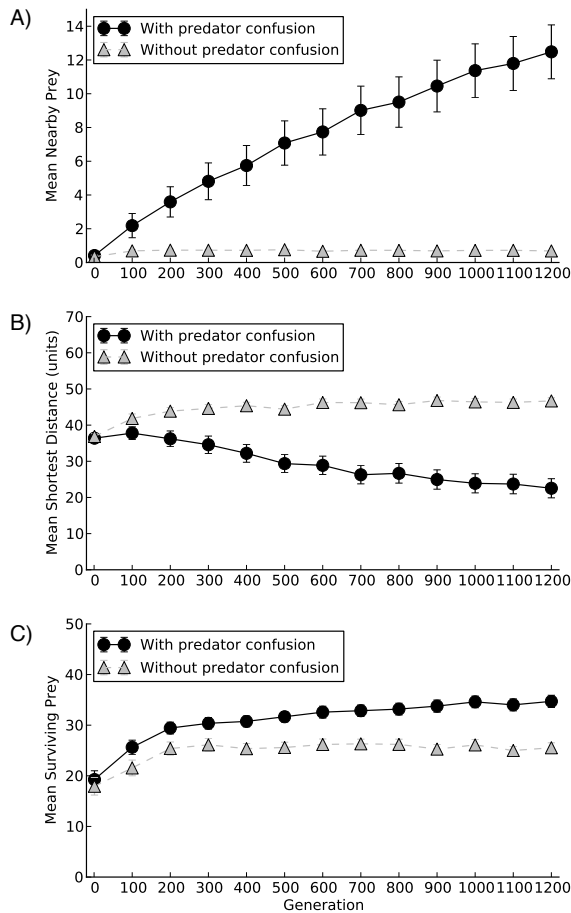


Fig. 3. Mean swarm density (A), swarm dispersion (B), and survivorship (C) within the swarm over all replicates over evolutionary time. The swarm density was measured by the mean number of prey agents within 30 units of each other over a lifespan of 2,000 simulation time steps. Swarm dispersion was measured by the mean distance to the nearest prey agent for every living prey agent over a lifespan of 2,000 simulation time steps. Survivorship within the swarm was measured as the mean number of surviving prey agents (out of an initial total of 50) at the end of the simulation at a given generation. Prey agents hunted by a predator with predator confusion (black circles with a full line) evolved to maintain significantly higher swarm density and significantly less dispersed swarming behavior than prey agents in the swarms hunted by a predator without predator confusion (grey triangles with a dashed line). As a result, significantly more prey agents survived in the swarms hunted by a predator with predator confusion than the swarms hunted by a predator without predator confusion. Error bars indicate two standard errors across 180 replicate experiments.

ior, where the predator just made a kill on the top-right edge of the top-rightmost swarm (kill location denoted by a black star). Videos of the evolved swarms under predation are available in the supplementary information (SI videos 1-5).

To evaluate the evolved swarms quantitatively, we obtained the line of descent (LOD) for every replicate by tracing the ancestors of the most-fit prey agent in the final population until we reached the randomly-generated ancestral agent with which the starting population was seeded (see [23] for an introduction to the concept of an LOD in the context of digital evolution). For each ancestor in the LOD, we characterized the swarm behavior with two common behavior measurements: *swarm density* and *swarm dispersion* [39]. We measured the swarm density as the mean number of prey agents within 30 units of each other over a lifespan of 2,000 simulation time steps. The swarm's dispersion was computed by averaging the distance to the nearest prey agent for every living prey

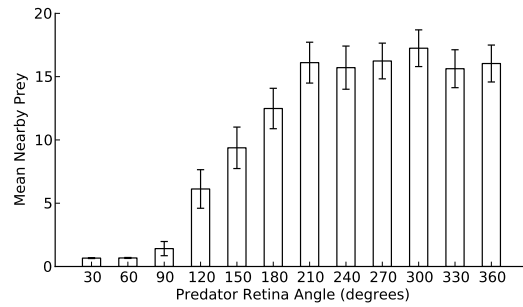


Fig. 4. Mean swarm density at generation 1,200 as a function of predator view angle. Swarming to confuse the predator was an ineffective behavior if the predator agent's visual field covered only the frontal 60° or less, due to the predator agent's focused retina. As the predator agent's visual field was incrementally increased to cover the frontal 90° and beyond, predator confusion via swarming again became an effective anti-predator behavior, as evidenced by the swarms exhibiting significantly higher swarm density at generation 1,200. Error bars indicate two standard errors across 180 replicate experiments.

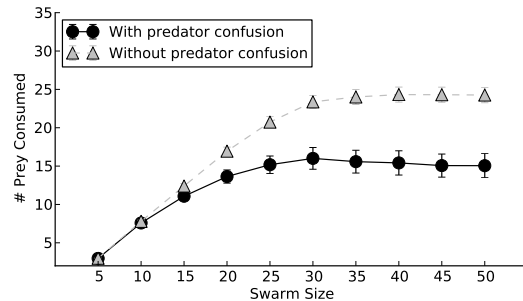


Fig. 5. Functional response curves of cohesive swarms hunted by a predator with predator confusion (black circles with a full line) and dispersed swarms hunted by a predator without predator confusion (grey triangles with a dashed line). The evolved, cohesive swarms hunted by a predator with predator confusion result in a Type II functional response with a lowered plateau. Error bars indicate two standard errors across 180 replicate experiments.

agent over a lifespan of 2,000 simulation time steps. Together, these metrics captured whether or not the prey agents were cohesively swarming.

Figure 3A demonstrates that the prey agents hunted by a predator without predator confusion moved close to each other by chance but never coordinated their movement at any point in their evolutionary history (mean swarm density ± 1 standard error across 180 replicates: 0.69 ± 0.02). In contrast, when hunted by a predator with predator confusion, the agents purposefully coordinated their movement to remain close to each other and form a swarm (mean swarm density 12.48 ± 0.8 at generation 1,200). Likewise, Figure 3B shows that in the absence of predator confusion, prey evolved to maximize their dispersion (mean shortest distance 46.69 ± 0.44 at generation 1,200), whereas with predator confusion, prey agents evolved increasingly cohesive swarm behavior (mean shortest distance 22.54 ± 1.32 at generation 1,200). Taken together, these results suggest that predator confusion provided a sufficient selection pressure to evolve cohesive swarming behavior in this model.

Figure 3C shows that as a result of these evolutionary trends, the cohesive swarms that evolved under predator confusion experienced significantly higher survivorship than swarms that evolved without predator confusion (34.7 ± 0.6 and 25.54 ± 0.49 prey surviving the simulations, respectively).

This increased survivorship confirms that swarming behavior confused the predator, leading to fewer successful kills.

Evolved Predator and Prey Agent Behavior. To deduce how swarms emerge in our model from individual-level behaviors, we had to determine the functionality of the evolved agent MNBs. We accomplished this by first visualizing the MNB connectivity to discern which slices of the retina and memory nodes of the MNB were causally connected, then created a truth table from the MNB mapping every possible input combination with its corresponding most-likely output from the MNB. With this input-output mapping, we computed the minimal descriptive logic of the MNB with hardware logic optimization software. We had to use the most-likely output for every input combination due to the stochastic nature of MNBs, therefore the functionality we determined was the *most-likely* behavior of the predator or prey agent.

In all of our experiments, the prey agents at generation 1,200 ignored the predator-sensing portion of their retina and instead concentrated on one or two slices of the conspecific-sensing retina to follow the other prey agents in the swarm. This was particularly striking because it suggested that prey can evolve swarming behavior in response to predation without the ability to sense the predators hunting them. We observed that the prey agents evolved a wide variety of simple algorithms that exhibited a diversity of emergent swarming behaviors, such as single cohesive swarms, single elongated swarms, multiple swarms that remained separated, and multiple swarms that merged into a single swarm during their lifetime. Videos of each of these swarm behavior types are available as SI videos 2-5.

As for the predators, the evolved behavior we observed at generation 1,200 in the predator confusion treatment appeared to be rather complex: the predator agent avoided dense swarms and hunted prey agents outside, or on the edge, of the swarm. However, the algorithm underlying this behavior was relatively simple. The predator agents only watched the two center retina slices and constantly turned in one direction until a prey agent entered one of those slices. Once a prey agent became visible in one of the center retina slices, the predator moved forward and pursued the prey agent until it made a kill attempt. This was repeated regardless of whether the predator achieved a successful kill. The simplicity of the predator algorithm and relative simplicity of the prey algorithms supports the findings of earlier digital swarm studies that complex swarm behaviors can be described by simple rules applied over a group of locally-interacting agents [40,41].

Effects of Predator Retina Angle. We implemented predator confusion by imposing a perceptual constraint that reduces the probability of successfully making a kill if one or more prey near the target prey are visible to the predator. This is analogous to placing a limit on the acuity of the visual system preventing the discrimination of one prey from another. To examine the effect of relaxing this constraint, we coevolved the predator and prey again and experimentally reduced the size of the predator's field of view, which is akin to improving acuity. Figure 4 demonstrates that when the predator agent's retina only covered the frontal 60° or less, swarming to confuse the predator was no longer a viable adaptation (as indicated by a mean swarm density of 0.68 ± 0.02 at generation 1,200): the predator had such a narrow view angle that few swarming prey were visible during an attack, thereby minimizing the confusion effect. As the predator agent's retina was incrementally modified to cover the frontal 120° and beyond, swarming again became an effective adaptation against the predator due

to the confusion effect (indicated by a mean swarm density of 6.13 ± 0.76 at generation 1,200). This suggests that the predator confusion mechanism may not only provide a selective pressure for the prey to swarm, but it could also provide a selective pressure for the predator to narrow its view angle to become less easily confused.

Effects on Functional Response. Predator confusion has been hypothesized to be not only a selective pressure favoring swarming, but also as a determinant of the *functional response* [35], i.e., the number of prey consumed by the predator as a function of prey density [36]. Figure 5 supports a key prediction of functional response theory: both with and without predator confusion, the system displayed a Type II functional response (a saturating effect of prey density), but when predator confusion was present the functional response showed a lower plateau (plateau at 24.01 ± 0.49 without predator confusion; 15.18 ± 0.57 with predator confusion). The fact that there was a Type II functional response even in the condition without predator confusion was presumably the result of an additional constraint present in both conditions: the kill delay that was imposed on the predator after prey capture before it can attack again.

Discussion

We demonstrated that swarming evolves as an emergent behavior in prey when a simple perceptual constraint—predator confusion—is imposed on the predator. We found that measuring swarm density and swarm dispersion, proposed in [39], serves as an effective substitute for qualitatively assessing every swarm to determine if cohesive swarming behavior is present. A diverse collection of prey swarming behaviors evolved in our model, suggesting that predator confusion allows a wide range of swarm behaviors to evolve. Strikingly, most evolved prey strategies used algorithms that responded to other prey, but not to the attacking predators. In contrast to the diversity of evolutionary outcomes for prey, a common behavioral strategy emerged among the predators when evolved in the confusion condition: namely, attacking the vulnerable edges of the swarms, a phenomenon commonly seen in nature [37,38].

We also found that we could reduce the advantage of swarming by shrinking the predator's field of view, hence decreasing the level of confusion affecting the predator. This suggests that predator confusion could impose a selective pressure on the shape of the predator's retina: once swarming has evolved in the prey, selection will favor predators that are no longer confused by swarms. Following the trend in Figure 4, we would expect selection to favor predators with narrower, more frontally focused retina, as observed in the visual systems of many natural predators [42].

Modeling functional response has been an important problem in ecology [43], and is critical for constructing accurate models that capture the dynamics of predator-prey interactions over ecological and evolutionary time [44]. We provided evidence that predator confusion has significant effects on functional response that are not captured in traditional models. Most of these traditional models, including the original formulation of Holling [30], capture the ecological interaction between predator and prey. Evolution is assumed to shape the behavioral strategies and constraints that influence predator-prey dynamics, but only recently have biologists begun to explicitly study the dynamics of predator-prey interactions over both ecological and evolutionary time [31]. We have shown that a Type II functional response evolves even when it is not directly selected for, and the shape of the func-

tional response can be attributed to specific constraints such as handling time (akin to the kill delay in our system) and predator confusion [35].

Conclusion

We demonstrated that predator confusion provides a sufficient selective advantage for prey to evolve swarming behavior in a digital model. Predator confusion likely contributed to the evolution of swarming behavior in animals which were hunted by predators that were more agile, but relied on visual systems to track their prey. An important caveat, of course, is that predator confusion is by no means the only evolutionary pressure that could have led to the evolution of swarming [7]. Our results suggest that digital evolutionary systems can pro-

vide a powerful tool to tease apart the various hypothesized selective pressures underlying swarm behavior.

Materials and Methods

The code for this experiment is publicly available on github with an open-source license at <https://github.com/adamilab/eos-predator-confusion/> and the data (with IPython Notebook [45]) from the Results and SI are available at <http://adamilab.msu.edu/research-data/eos-predator-confusion.zip>. The Logic Friday logic optimization software used for MNB behavior analysis is available at <http://sontrak.com/>.

ACKNOWLEDGMENTS. We wish to acknowledge the support of Michigan State University High Performance Computing Center and the Institute for Cyber Enabled Research (iCER). This work was supported in part by the National Science Foundations BEACON Center for the Study of Evolution in Action, under Cooperative Agreement DBI-0939454.

- Couzin, ID (2009) Collective cognition in animal groups. *Trends in Cognitive Sciences* 13:35-43.
- Feare CJ (1984) *The Starling*. Oxford University Press, USA.
- Makris NC, Ratilal P, Jagannathan S, Gong Z, Andrews M, Bertsatos I, Godo OR, Nero RW, Jech JM (2009) Critical population density triggers rapid formation of vast oceanic fish shoals. *Science* 323:1734-1737.
- Symmons PM, Cressman K (2001) *Desert locust guidelines: biology and behaviour*. Rome: Food and Agriculture organization (FAO) of the United Nations.
- Kersten M, Britton RH, Dugan PJ, Hafner H (1991) Flock feeding and food intake in little egrets: the effects of prey distribution and behavior. *Journal of Animal Ecology* 60:241-252.
- Ballerini M et al. (2008) Interaction ruling collective animal behavior depends on topological rather than metric distance: evidence from a field study. *Proc. Natl. Acad. Sci. U. S. A.* 105:1232-1237.
- Krause J, Ruxton GD (2002) *Living in Groups*. Oxford University Press, USA.
- Diabate A, Yaro AS, Dao A, Diallo M, Huestis DL, Lehmann T (2011) Spatial distribution and male mating success of *Anopheles gambiae* swarms. *BMC Evolutionary Biology* 11:184.
- Yuval B, Wekesa JW, Washino RK (1993) Effect of body size on swarming behavior and mating success of male *Anopheles freeborni* (Diptera: Culicidae). *Journal of Insect Behavior* 6: 333-342.
- Pulliam HR, Caraco T (1984). Living in groups: is there an optimal group size? In *Behavioural Ecology: An Evolutionary Approach*, 2nd Ed., eds Krebs JR, Davies NB (Sinauer, Sunderland, Mass.), pp 122-147.
- Treherne JE, Foster WA (1981) Group transmission of predator avoidance behaviour in a marine insect: the Trafalgar effect. *Animal Behaviour* 29:911-917.
- Kenward RE (1978) Hawks and doves: Factors affecting success and selection in goshawk attacks on woodpigeons. *Journal of Animal Ecology* 47:449-460.
- Pulliam HR (1973) On the advantages of flocking. *Journal of Theoretical Biology* 38:419-422.
- Treisman M (1975) Predation and the evolution of gregariousness. I. Models for concealment and evasion. *Animal Behaviour* 23:779-800.
- Inman AJ, Krebs J (1987) Predation and group living. *Trends in Ecology & Evolution* 2:31-32.
- Treherne JE, Foster WA (1982) Group size and anti-predator strategies in a marine insect. *Animal Behaviour* 30:536-542.
- Foster WA, Treherne JE (1981) Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* 293:466-467.
- Hamilton WD (1971) Geometry for the selfish herd. *Journal of Theoretical Biology* 31:295-311.
- Bertram BRC (1978) In *Behavioral Ecology, An Evolutionary Approach* eds. Krebs JR, Davies NB (Blackwell Scientific, Oxford), pp. 6496
- Ioannou CC, Tosh CR, Neville L, Krause J The confusion effect—from neural networks to reduced predation risk. *Behavioral Ecology* 19:126-130.
- Jeschke JM, Tollrian R (2007) Prey swarming: which predators become confused and why? *Animal Behaviour* 74:387-393.
- Beauchamp G (2004) Reduced Flocking by birds on islands with relaxed predation. *Proceedings of the Royal Society London Series B* 271:1039-1042.
- Lenski RE, Ofria C, Pennock RT, Adami C (2003) The evolutionary origin of complex features. *Nature* 423:139-144.
- Wilke CO, Wang JL, Ofria C, Lenski RE, Adami C (2001) Evolution of digital organisms at high mutation rates leads to survival of the flattest. *Nature* 412:331-333.
- Lukeman R, Li YX, Edelstein-Keshet L (2010) Inferring individual rules from collective behavior. *Proc. Natl. Acad. Sci. U. S. A.* 107:12576-12580.
- Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. *Nature* 433:513-516.
- Couzin ID, Krause J, James R, Ruxton GD, Franks NR Collective memory and spatial sorting in animal groups. *Journal of Theoretical Biology* 218:1-11.
- Krakauer DC (1995) Groups Confuse predators by exploiting perceptual bottlenecks: A Connectionist model of the confusion effect. *Behavioral Ecology and Sociobiology* 36:421-429.
- Humphries DA, Driver PM (1970) Protean defence by prey animals. *Oecologia* 5:285-302.
- Holling CS (1959) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* 91:385-398.
- Hairston NG, Ellner SP, Geber MA, Yoshida T, Fox JA (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters* 8:1114-1127.
- Edlund JA, Chaumont N, Hintze A, Koch C, Tononi G, Adami C (2011) Integrated information increases with fitness in the evolution of animats. *PLoS Computational Biology* 7:e1002236.
- Goldberg DE (1989) *Genetic Algorithms in Search, Optimization, and Machine Learning*. Addison-Wesley.
- Martin GR (1986) The eye of a passeriform bird, the European starling (*Sturnus vulgaris*): eye movement amplitude, visual fields and schematic optics. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 159:545-557.
- Jeschke JM, Tollrian R (2005) Effects of predator confusion on functional responses *Oikos* 111:547-555.
- Murdoch WW (1973) The functional response of predators. *J. Appl. Ecol.* 10:335-342.
- Hirsch BT, Morrell LJ (2011) Measuring marginal predation in animal groups. *Behavioral Ecology* 22:648-656.
- Romey WL, Walston AR, Watt PJ (2008) Do 3-D predators attack the margins of 2-D selfish herds? *Behavioral Ecology* 19:74-78.
- Huepe C, Aldana M (2011) New tools for characterizing swarming systems: A comparison of minimal models. *Physica A: Statistical Mechanics and its Applications* 387:2809-2822.
- Spector L, Klein J, Perry C, Feinstein M (2005) Emergence of collective behavior in evolving populations of flying agents. *Genetic Programming and evolvable machines* 6:111-125.
- Reynolds CW (1987) Flocks, herds and schools: A distributed behavioral model. *Proceedings of the 14th annual conference on Computer graphics and interactive techniques* 25-34.
- Tucker VA (2000) The deep fovea, sideways vision and spiral flight paths in raptors. *Journal of Experimental Biology* 203:3745-3754.
- Solomon ME (1949) The Natural Control of Animal Populations. *Journal of Animal Ecology* 18:1-35.
- Jeschke JM, Kopp M, Tollrian R (2004) Consumer-food systems: why type I functional responses are exclusive to filter feeders. *Biological Reviews* 79:337-349.
- Perez F, Granger BE (2007) IPython: A system for interactive scientific computing. *Computing in Science and Engineering*, 9:21-29.